Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations

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Although several studies have shown genetic differences between hatchery and wild anadromous Pacific salmon (*Oncorhynchus* spp.), none has provided compelling evidence that artificial propagation poses a genetic threat to conservation of naturally spawning populations. When the published studies and three studies in progress are considered collectively, however, they provide strong evidence that the fitness for natural spawning and rearing can be rapidly and substantially reduced by artificial propagation. This issue takes on great importance in the Pacific Northwest where supplementation of wild salmon populations with hatchery fish has been identified as an important tool for restoring these populations. Recognition of negative aspects may lead to restricted use of supplementation, and better conservation, better evaluation, and greater benefits when supplementation is used.

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Introduction

Artificial propagation has been identified as an important tool for increasing wild (naturally spawning) populations of anadromous Pacific salmon (*Oncorhynchus* spp.; NPPC, 1992). Target populations should be those that are: (1) otherwise likely to become extinct within a few generations (e.g. Fleming, 1994), or (2) substantially below carrying capacity (Waples, 1991; NRC, 1996). The juvenile hatchery fish for such programmes are typically released away from the hatchery so that after migrating to sea and returning to fresh water as adults they spawn in natural spawning areas. Alternatively, returning adult hatchery fish may be released into natural spawning areas. Interbreeding of hatchery fish and wild fish is an intended outcome of either type of supplementation.

Clearly, artificial propagation can play a valuable role in conservation. The high survival rates often achieved may temporarily sustain a wild population at risk of extinction until environmental improvements can be effected and the population can persist on its own. Even so, any negative consequences from artificial propagation must also be recognized. While artificial propagation may temporarily solve demographic problems, it may cause genetic and harvest changes (McIntyre and Reisenbichler, 1986; Waples, 1991; Utter et al., 1993; Campton, 1995) which might increase the risk of extinction once supplementation ends (Currens and Busack, 1995). In situations other than where a population faces imminent extinction, questions concerning conservation or economic efficiency require that the positive aspects be weighed against the negative aspects in deciding whether to initiate artificial propagation, or in selecting appropriate levels of supplementation.

Here we focus on just one of the negative effects from artificial propagation: genetic changes that reduce population fitness for natural propagation (hereafter abbreviated "fitness"). Although such changes may reduce the productivity and viability of a population for natural rearing, the potential hazards have not been universally accepted as real or relevant to management of Pacific salmon (Lichatowich et al., this issue). Much of this

scepticism stems from the diadromous life history of these fish. Culture of Pacific salmon primarily involves sea ranching where the fish are reared in captivity only during freshwater juvenile stages. Subsequently, the juveniles are released to migrate to sea and utilize the food supplies provided by the marine environment. Substantial genetic change and corresponding loss of fitness have seemed unlikely for populations experiencing natural conditions during most of their life cycle.

Apparent loss of fitness in hatchery populations of resident trout (non-anadromous *Oncorhynchus* spp., *Salmo* spp., and *Salvelinus* spp.) compared to proximate wild populations was demonstrated long ago (e.g. Greene, 1952; Flick and Webster, 1964), consistent with the genetic change generally expected from domestication of captive populations (Kohane and Parsons, 1988). This evidence for genetic change has been easily and widely accepted because hatchery trout are typically reared from conception through sexual maturity and experience no natural selection beyond the hatchery conditions. In contrast, sea-ranched Pacific salmon are typically exposed to natural selection in the natural environment for two-thirds or more of their life as they migrate downstream, grow in the sea, and then return to fresh water at maturity. As mortality in the hatchery is usually very low, there is reluctance to accept that the genetic fitness of hatchery populations to produce viable fry under natural conditions declines rapidly or substantially. According to this view, interbreeding of hatchery fish with wild fish should not compromise the wild population (e.g. Cuenco, 1994).

We argue that published information and three studies in progress collectively provide compelling evidence that (traditional) artificial propagation of steelhead (*Oncorhynchus mykiss*), stream-type chinook salmon (*O. tshawytscha*; Healey, 1991), coho salmon (*O. kisutch*), and probably other Pacific salmon results in significant genetic change which lowers fitness. When such fish spawn naturally with wild fish, the productivity and viability of the naturally spawning population declines substantially. The implications for conservation and economic efficiency are important.

General evidence of genetic change

At least eight published studies have shown genetic differences between hatchery (sea ranched) and wild populations of anadromous Pacific salmon in behavioural or physiological traits that should reduce the fitness of hatchery fish (Table 1). Genetic information provided by electrophoresis and molecular techniques are not discussed because they tell very little about the adaptive characteristics of a population (Utter *et al.*, 1993). Development rate may change in response to novel temperature regimes; time of spawning and growth rate may change due to either artificial selection or natural selection (Reisenbichler and McIntyre, 1986); and agonistic behaviour may increase, territorial behaviour decrease, and predator avoidance decrease in response to unnatural community and trophic conditions in the hatchery. Reluctance to accept that these genetic changes are caused by the hatchery programme probably stems from obvious limitations of individual studies which may restrict the generality of their results. The two primary limitations are that: (1) only one or a few aspects of behaviour or life history were examined in each study, and (2) hatchery populations were not always derived from the wild populations used in the comparison. The latter point is problematic because wild stocks differ genetically among themselves (e.g. Taylor, 1991), and the same is true for hatchery stocks (Reisenbichler, 1988). So the differences between hatchery fish and wild fish in five of the eight studies were confounded with differences in ancestral stock. As a consequence of such limitations, constructive debate and consensus on how to avoid deleterious genetic effects from artificial propagation have been limited or ineffectual, often because participants haven't agreed that the problem exists.

We submit three reasons for concluding that artificial propagation reduces fitness despite the above limitations. First, the confounding of hatchery–wild differences with differences in ancestry probably had little effect, at least qualitatively, on the results. Hjort and Schreck (1982), Taylor (1986), and Fleming and Gross (1989) found that hatchery stocks were more similar in morphology and life history to each other than to wild stocks across ranges of several hundred kilometres. Likewise, wild stocks were more similar to each other than to hatchery stocks. These results indicate a similarity of environmental conditions among hatcheries, and a substantial difference between conditions in hatcheries and those in natural streams within the same region. Accordingly, natural selection in hatchery populations should operate to produce genetic adaptations which are similar among hatcheries, but distinct from the genetic adaptations of wild populations. Therefore, comparing a hatchery population to proximate wild populations should provide results similar to a comparison with its ancestral wild population. Note that the results from the confounded studies agree with those where the hatchery and wild populations were of common ancestry.

Second, the results from genetic comparisons of hatchery and wild salmon are consistent with expectations from evolutionary theory. The environmental conditions (hence the selective pressures) in the traditional hatchery differ greatly from those in the natural system:

- quantity, delivery schedule, and composition of food;

Table 1. A synopsis of studies that show genetic differences in behaviour (B) or physiology (P) between hatchery (sea ranched) populations (H) and wild populations (W) of anadromous salmonid fishes. Factors limiting the validity for extrapolating the results to other populations and species are listed.

Study; trait type; species	Description	Limitations
Lannan, 1980. P – embryo and larval development rate. *Oncorhynchus keta*	Thermal units (°F-days) from fertilization to emergence increased from 1800 to 2350 during 1972–1977 in H established in 1969 from local W. Higher temperatures in hatchery than in stream initially resulted in early, apparently mal-adaptive time of entry to estuary. Presumably, natural selection acted to retard development rate so that entry period of H coincided more closely with original entry period of W.	No parallel data through time were presented for W; no control.
Nickelson *et al.*, 1986. P – spawning time. *Oncorhynchus kisutch*	Fed H fry released into natural streams and allowed to spawn naturally with W when they returned. H spawned substantially earlier than W. From subsequent juvenile abundances, the authors inferred that reproductive success for H was almost zero, and attributed this largely to the early spawning time.	H did not originate from W. H and W did not share common environment their entire lives. Artificial selection at least partially responsible for advanced spawning time. Reproductive success not measured directly.
Norman, 1987 (as cited by Utter *et al.*, 1993). B – territoriality. *Salmo salar*	Progeny of H displayed weaker territorial behaviour than did progeny of W.	H did not originate from W.
Swain and Riddell, 1990. B – aggression. *Oncorhynchus kisutch*	Juveniles from two H more aggressive in mirror-image stimulation tests than W from geographically proximate populations. Each H compared with two W.	H did not originate from W.
Berejikian *et al.*, 1996. B – aggression. *Oncorhynchus mykiss*	Progeny of W more aggressive at emergence than of locally derived H. Progeny of H more aggressive than of W after rearing for 3 months in natural stream channel or in tanks at low densities and low rations.	None obvious.
Berejikian, 1995. B – predator avoidance. *Oncorhynchus mykiss*	Juveniles of W survived predation from prickly sculpin (*Cottus asper*) better than did size-matched progeny from locally derived H, both in laboratory and natural stream enclosures.	None obvious.
Johnsson *et al.*, 1996 P/B – growth, predator avoidance. *Salmo trutta*	Progeny of W less susceptible to a trout predator than were progeny from a locally derived H. Progeny of H grew faster in hatchery, and had lower RNA levels.	None obvious.
Kallio-Nyberg and Koljonen, 1997. P – growth and maturity. *Salmo salar*	Progeny of H grew faster in hatchery and at sea, and more frequently matured as grilse than did progeny of W.	H only partially derived from W.

- quantity and type of cover, contour and diversity in composition of substrate, and water depth and velocity;
- density of conspecifics and densities and species composition of competitors, predators, and disease organisms;
- even the water often differs in chemistry, temperature, and turbidity.

Population genetics theory (e.g. Hartl, 1980) predicts that when two initially identical populations are held separately in substantially different environments, and additive genetic variation exists for adaptive traits, the populations will change genetically as they adapt to the respective environments. The observed genetic differences between hatchery and wild fish (Table 1) attest to the presence of additive genetic variation for such traits; however, large or rapid genetic changes in fitness seem unlikely without substantial selective mortality. The typically low mortality in many hatcheries (frequently less than 15%) has often led to the conclusion that large

or rapid, inadvertent genetic change cannot occur.
Intense selection, however, may occur through the very
high mortality (often greater than 95%) after release.
This mortality apparently selects against fish that are
poorly adapted to the hatchery environment. For
example, offspring of hatchery steelhead grow faster in
the hatchery than do the offspring of wild steelhead
under identical conditions (Reisenbichler and McIntyre,
1977) probably because survival after release is strongly
and positively related to size at release (Wagner et al.,
1963). Selection after release apparently favours those
individuals that are genetically predisposed to grow well
in the hatchery. Nine-hundred progeny of wild steelhead
reared in a hatchery in Idaho were marked with unique
tags before the fish were released in 1997. Less than 1%
of the fish that were below median size at the time of
release were recovered at downstream dams as com-
pared to 30% for the fish that were above median size
(US Geological Survey, unpubl. data). The 30-fold
difference in recovery rate reflects selection intensity
sufficient to effect substantial genetic change in the
population.

Finally, the results from genetic comparisons of
hatchery and wild salmon (Table 1) are consistent with
studies of resident and farmed salmonids (which spend
their entire lives in captivity; see reviews in Utter et al.,
1993; Campton, 1995; Einum and Fleming, 1997;
McGinnity et al., 1997), and with studies of other
organisms which have shown substantial genetic
adaptation (i.e. domestication) in response to artificial
conditions (Kohane and Parsons, 1988; Frankham and
Loebel, 1992). All observed differences suggest that
hatchery salmonids are genetically inferior to wild
salmonids in respect of natural production.

Evidence for differential survival of progeny

Two published studies and three in progress involve tests
for genetic differences in survival between progeny of
(sea ranched) hatchery fish and of wild fish residing in
natural waters. For brevity, progeny will be called
hatchery or wild depending on their parentage not their
environment. The two groups were released into the
same streams or hatchery ponds so that observed differ-
ences in performance would reflect genetic differences,
not environmental differences. All five studies found that
the survival of hatchery fish was less than that for wild
fish.

Reisenbichler and McIntyre (1977) studied one year
class of summer steelhead in four small streams in the
Deschutes River basin, Oregon. The hatchery popula-
tion originated from the wild population in the
Deschutes River and had been cultured only two
generations, reputedly without any selective breeding.
The comparisons extended from release as eyed-embryos
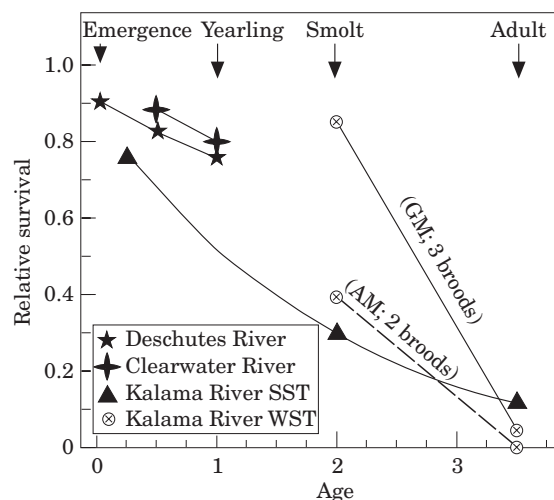or button-up fry to age-1 (about 12 months), and

Figure 1. Relative survival of progeny of hatchery to wild
steelhead in natural streams (or at sea) at various ages. Relative
survivals were evaluated from the eyed-embryo stage in
Oregon's Deschutes River (Reisenbichler and McIntyre, 1977),
unfertilized eggs in Washington's Kalama River (Leider et al.,
1990; Hulett et al., 1996), and swim-up fry in Idaho's Clear-
water River (US Geological Survey, unpubl. data). Data for the
Kalama River summer steelhead are arithmetic means from the
four year classes. Preliminary data for the Kalama River winter
steelhead are the geometric means (GM) for three year classes,
or the arithmetic means (AR) for two year classes with the
exceptionally high year class omitted (see text). Curves were
fitted by eye.

showed that survival of hatchery fish was less than that
of wild fish (relative survival was less than one; Figure
1). Intermediate survivals for hybrids (all progeny of
wild males and hatchery females) showed that genetic
differences, not maternal effects, accounted for the
observed differences. Additional experimental fish were
reared together in the hatchery where hatchery fish
survived and grew best.

Leider et al. (1990) studied four year classes of sum-
mer steelhead in the Kalama River, Washington state.
The wild adults were from the Kalama River. The
hatchery stock was from the Washougal River, was
developed with fish from the Washougal and Klickitat
Rivers primarily, and had been cultured six generations.
All three streams are tributaries of the lower Columbia
River. Genetically marked hatchery fish were released as
smolts, and returned as adults several years later. Wild
and returning hatchery adults were enumerated and
allowed to spawn naturally. The relative survivals of
their progeny were evaluated as juveniles and as return-
ing adults. The reproductive success of hatchery adults
was lower than of wild adults, and relative survival of
hatchery fish consistently declined through successive
life history stages (Figure 1). Apparently, genetic differ-
ences in fitness were not eliminated after a brief initial
period of differential mortality, but persisted at least

beyond the first 2 yrs of life when the juveniles migrate to sea, and perhaps to maturity.

Hulett *et al.* (1996) studied three year classes of winter steelhead in the Kalama River. The wild adults were from the local population while the hatchery population was from the Elochoman River and had been cultured 10 generations. The hatchery population was primarily developed with fish from the Elochoman and Cowlitz Rivers (tributaries of the Lower Columbia River) but also included fish from Chambers Creek (tributary to Puget Sound). Genetically marked hatchery fish were released as smolts and returned as adults several years later. Wild adults and returning hatchery adults were enumerated and allowed to spawn naturally. Relative survivals of their progeny were evaluated as smolts and as returning adults. This study found that the relative survival of hatchery fish was much less than that of wild fish (Figure 1). Two of the three year classes provided results very similar to those from Leider *et al.* (1990), while for the other year class relative survival of hatchery fish to the smolt stage was 4.5. Nevertheless, hatchery fish of this year class suffered much greater mortality after the smolts emigrated from the river so that the relative survival between conception and maturity was about 0.2, similar to values from Leider *et al.* (1990)

We are studying two year classes of summer steelhead in the Clearwater River system, Idaho. Both the hatchery and wild populations were from the Clearwater River, but the former originated from wild fish in the North Fork Clearwater River, and the latter were from tributaries of the Middle Fork. The hatchery population had been cultured six generations, and selective breeding was avoided except perhaps for time of return to the hatchery in some early years. Comparisons were made from release as button-up fry to age-1, and showed reduced survival of hatchery fish (Figure 1). The study is in progress and results are preliminary. The two groups also were reared together in hatcheries where the hatchery fish grew and survived better than did wild fish.

We also are studying stream-type chinook salmon (Healey, 1991) in the Little White Salmon River, a tributary to the Columbia River about 60 km downstream from the Deschutes River. Both the hatchery population and the wild population were from the Warm Springs River, a tributary to the Deschutes River. The hatchery population originated from the wild population, and had been cultured for four generations. The juveniles are incubated and reared in the hatchery for 13 or 19 months before they are released and migrate to sea. Wild fish comprised 100% of the hatchery's brood fish each of the first four brood years, 10–76% (mean of 38%) for 1982–1990, 0% for 1991, 10% for 1992, and 0% for 1993 (Olson *et al.*, 1995). Over 90% of the adults providing gametes for our study were from the 1992 brood year; the remainder were from the 1991 and 1993 brood years. Hatchery personnel reputedly avoided

selective breeding. The comparison was from January 1997, when the experimental fish were released as button-up fry, to August 1997, and showed relative survival of hatchery fish to be 0.86. Work with this year class will not be completed until after the smolt migration in spring 1998, so the results are preliminary.

Although these studies have various limitations which undoubtedly bias the magnitude of the observed differences between hatchery and wild fish, we judge the qualitative conclusions to be robust. The studies with steelhead from the Deschutes and Clearwater Rivers and spring chinook salmon only covered the early life of the cohorts, so relative survival of hatchery fish measured over the entire life of the cohort should have been even lower (Figure 1). The study stream for the spring chinook salmon was not in the drainage from which the hatchery and wild populations originated, and wild fish had been continually infused into the hatchery population to avoid genetic change in the latter. We do not know the effect of study stream but consider it to be minor. Continual gene flow from the wild population should have caused the decline in survival to be less than would have resulted without this gene flow.

Disregarding the different ancestral origin of the hatchery fish, three factors might limit the relevance of the Kalama River studies for quantifying loss of fitness from domestication. First, wild adults, unlike hatchery adults, resulted from successful spawning and growth in the river which might have helped them home to the best locations. Second, hatchery adults on average spawned about 1 month earlier than did wild adults which may have reduced reproductive success to the early life-history stages (Reisenbichler, 1997). Advanced spawning time is not a necessary consequence of hatchery programmes (e.g. Reisenbichler and McIntyre, 1986). Nevertheless, "differential mortality to the sub-yearling stage had a relatively minor influence on estimates of overall differential mortality to the smolt stage" (Leider *et al.*, 1990), so these first two factors are of minor consequence. Indeed, two year classes of hatchery fish (one of winter steelhead; one of summer steelhead) survived better to the sub-yearling or smolt stages than did wild fish, yet overall survivals to returning adult for both year classes were low and similar to those for the other year classes. Third, hatchery fish had been spawning in the Kalama River in prior years, and at least some wild fish may have had hatchery fish as parents. Any effect due to prior introgression from hatchery fish should mean that wild fish would have survived even better without such introgression, and relative survival for hatchery fish would have been lower.

Conclusions

All five of the studies in natural streams suggest the same conclusion: hatchery programmes that rear steelhead or

chinook salmon for 1 year or longer before release genetically change the population and thereby reduce reproductive success when these fish spawn in natural systems. The results are consistent and confirm the results from the eight studies summarized in Table 1, which included additional species and work on two continents. In view of this consistency, one conclusion seems obvious: substantial genetic change in fitness results from traditional artificial propagation of anadromous salmonids held in captivity for one-quarter or more of their life. Although almost no comparable data are available for coho salmon or sockeye salmon (*O. nerka*), which typically spend more than one-third of their life in fresh water, it seems prudent to assume that the same conclusion holds. To date almost no comparable data are available for species or populations which are held in captivity for shorter portions of their life: pink salmon (*O. gorbuscha*), chum salmon (but see Table 1), ocean-type chinook salmon (less than a year of freshwater residence; Healey, 1991), and some sockeye salmon populations. Nevertheless, similar though smaller genetic changes for these fish may be expected.

These conclusions imply that supplementation (wherein wild fish interbreed with hatchery fish of reduced fitness) will reduce the productivity of naturally spawning populations, and often may compromise conservation objectives. Relative survival of hatchery steelhead continued to decline with age of the cohort, at least until after emigration as smolts (Figure 1). This decline suggests that the fitness of the next generation would be low even before interbreeding with more hatchery fish, and that continuous supplementation should progressively diminish the productivity of the naturally spawning population. The typical population proposed for supplementation is presumably one of low productivity which is substantially below carrying capacity. Continued supplementation of such a population may reduce its productivity so that the population even becomes dependent on supplementation and cannot replace itself otherwise (Figure 2). Note here that other potential genetic effects are not considered. Additional effects include the possible loss of local adaptations from genetic homogenization when the supplemented population consists of subpopulations (e.g. Bowles, 1995), and inadvertent reductions in effective population size (Ryman and Laikre, 1991). Decisions must be taken whether the risk of degradation from supplementation is acceptable, and if so, for how many of the naturally spawning populations. The benefits (production) from a supplementation programme may be less, perhaps much less, than those expected without consideration of genetic changes.

The two studies comparing hatchery and wild fish in streams and in hatcheries provide firm evidence that the genetic change from artificial propagation, in large part, results from natural selection for fish that are well-
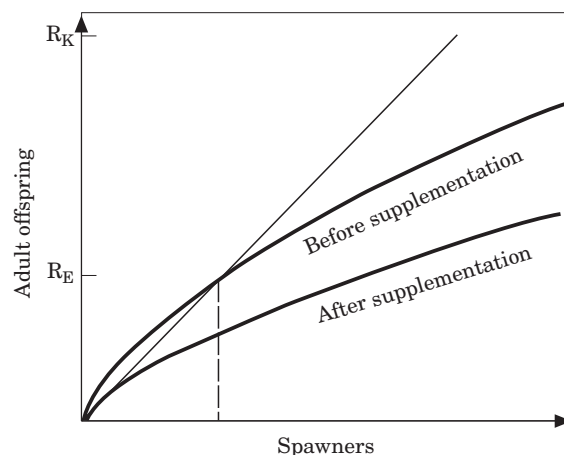

Figure 2. Hypothetical reproductive relations for a naturally spawning population before and after prolonged supplementation. The upper curve depicts a wild population of low productivity, far below its carrying capacity (maximum recruitment level, R_k). The diagonal line indicates where the number of progeny equals the number of spawners, and identifies R_E as the equilibrium population size before supplementation. Note that after supplementation, the population cannot replace itself and may then require supplementation to persist.

adapted to the hatchery environment, i.e. from domestication selection. Alternative explanations seem unlikely. If relaxed selection had been the predominant agent responsible for genetic change (Waples, 1991), wild fish should have performed as well or better in the hatchery. If genetic change from small population size in the hatchery had been the predominant agent, wild fish should have done better in the hatchery. Inasmuch as hatchery fish did better under hatchery conditions, we conclude that relaxed selection or small population size had, at most, minor effects in these studies.

Apparently domestication selection is often intense. The fitness of stream-type chinook salmon was diminished after four generations of culture, despite continuous gene flow from the wild population (on average, wild fish comprised 38% of the hatchery broodstock). The fitness of steelhead was diminished after only two generations in the hatchery (Reisenbichler and McIntyre, 1977). Presumably substantial change occurs in the first generation.

The management significance of domesticaiton selection is that simply changing mating protocols (e.g. Allendorf and Ryman, 1987) will not eliminate genetic change from artificial propagation. If domestication is to be reduced or eliminated, the hatchery environment and other practices must be modified. Although alternative mating protocols have been identified (Allendorf, 1993), and more natural rearing systems are under development (Maynard *et al.*, 1995), their effect on domestication selection has yet to be evaluated, and it would be

imprudent to assume that they will eliminate the problem (Meffe, 1992).

Substantial declines in fitness for natural propagation are clearly undesirable both for conservation and the economic efficiency of supplementation. General recognition that the problem exists should facilitate broader or rapid application of various responses to avoid or reduce negative consequences of artificial propagation. Such responses include: (1) explicitly including genetic effects when estimating benefit:cost ratios for deciding whether to supplement; (2) restricting the number of hatchery fish used for supplementation; (3) restricting the number of wild populations to be supplemented; (4) using only wild fish as broodstock; (5) creating more natural artificial rearing environments (selective regimes) (Maynard *et al.*, 1995); and (6) modifying protocols to reduce mortality or differential reproductive success (e.g. Allendorf, 1993).

It should be recognized that the efficacies for most of these responses are uncertain. For example, it is not known whether using only wild fish is the best broodstock management strategy. The only responses known to substantially reduce the problem are restricting the number of hatchery fish and restricting the number of populations supplemented, i.e. designating a substantial proportion of the viable wild populations to remain completely wild.

Acknowledgements

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